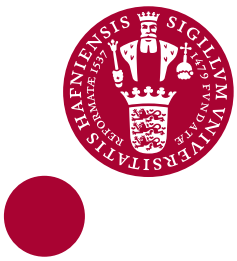

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RESEARCH ARTICLE

Genetic population structure of harbour seals in the United Kingdom and neighbouring waters

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Abstract

1. In the United Kingdom (UK), several harbour seal (*Phoca vitulina*) populations have been declining over the past decade. In order to understand the effect of these changes in abundance, this study seeks to determine the population structure of harbour seals in the UK, and in Scotland in particular, on a wider and finer spatial scale than has previously been reported.
2. Harbour seals were genotyped from 18 different localities throughout the UK and neighbouring localities in mainland Europe, at 12 microsatellite loci. Results from Bayesian and frequency based tests of population structure suggested an initial structural division into two main groups consisting of localities in northern UK and southern UK–mainland Europe, respectively.
3. These two clusters were further divided into four geographically distinct genetic clusters.
4. An overall agreement between the genetic results and the existing management areas for UK harbour seals was observed, but it is also clear that an adaptive management approach should be adopted, in which the delineation of the current management areas is maintained until further genetic and ecological information has been accumulated and analysed.

KEYWORDS

coastal, genetics, mammal, microsatellite loci, Phoca vitulina, Seal Management Units

1 | INTRODUCTION

It is well recognized that information on the genetic population structure and levels of genetic variation within and between populations of a species are critical to its successful conservation and management. In particular, it enables the identification of discrete units that may be evolutionarily or ecologically important and thus require specific conservation and management strategies to ensure demographic stability and maintain biodiversity (Moritz, 1994; Waples, 1998; Waples & Gaggiotti, 2006).

The harbour seal is a small phocid seal found in temperate and subarctic regions across the Northern Hemisphere. Harbour seals are relatively philopatric and form multiple discrete populations across their range – some with geographic extensions measured in tens of kilometres, others in hundreds of kilometres, and often following seemingly distinct demographic trajectories (Andersen et al., 2011; Andersen & Olsen, 2010; Goodman, 1998; Olsen et al., 2014; Stanley et al., 1996; Westlake & O'Corry-Crowe, 2002).

Approximately 30% of the harbour seals in Europe occur in the UK (SCOS, 2014). They are widespread around the west coast of Scotland and throughout the Hebrides, Orkney and Shetland Islands

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(Supplementary Figure S1). In contrast, the distribution on the east coast is more or less restricted to the major estuaries of the Thames, The Wash, Firth of Tay and the Moray Firth. Overall, Scotland holds 79% of the UK harbour seal population, with 16% in England and 5% in Northern Ireland. The Irish population is about one-tenth the size of the UK population (SCOS, 2014). In the UK, harbour seal counts had been stable or increasing until about a decade ago, when declines were seen in Shetland by 30%, Orkney by 80% and the Tay Estuary by 90%. However, in other regions such as the Scottish west coast, the Outer Hebrides, Moray Firth and the English east coast counts have been stable or fluctuating. The causes of these declines are uncertain, but they are not thought to be related to the 2002 phocine distemper virus (PDV) epidemic (SCOS, 2014).

A critical first step in understanding and assessing the effects of changes in abundance is to identify groupings or units that, on both a temporal and spatial scale, are relevant for management and conservation efforts (Waples & Gaggiotti, 2006). Currently there are 11 defined harbour seal management units in the UK. The delineation of these was supported by extensive aerial survey count data collected during the harbour seal annual moult and information on movement patterns obtained from telemetry tagging programmes (SCOS, 2014; Sharples, Moss, Patterson, & Hammond, 2012). Still, there are questions that cannot be answered before a range-wide assessment of genetic population structure and diversity has been performed.

The only genetic assessment of harbour seal population structure to date that included the UK was based on seven microsatellite markers genotyped in samples from the 1988 PDV epidemic (Goodman, 1998). It investigated population structure on a pan-European scale and included four sampling sites in the UK (English east coast, Scottish east coast, Scottish west coast and Irish east coast). The results suggested the existence of six harbour seal populations in Europe, of which Scottish and Irish localities comprised one population, and the English east coast another (the remaining four being Iceland, Wadden Sea, western Scandinavia and the Baltic Sea). Given the strong site-fidelity of European harbour seals documented by both tagging (Dietz, Teilmann, Andersen, Rigét, & Olsen, 2012; SCOS, 2014; Sharples et al., 2012) and genetic studies (Olsen et al., 2014) it is likely that additional population structuring exists within the UK, and that the two Scottish–Irish and English east coast populations reflect evolutionary significant units (*senso* Moritz, 1994) rather than populations on the ecological or demographic scale appropriate for management (Lowe & Allendorf, 2010; Palsbøll, Bérubé, & Allendorf, 2007; Waples & Gaggiotti, 2006). The aim of this study was to guide management and conservation efforts by assessing the population structure of harbour seals in the UK, and in Scotland in particular, on a wider and finer spatial scale than previously.

2 | MATERIALS AND METHODS

2.1 | Sampling

Harbour seal skin samples were collected across the UK from live seals captured, sampled and released by the Sea Mammal Research Unit, University of St Andrews under their Animal (Scientific Procedures) Act 1986, Home Office Licence No. 60/4009. Animals were captured on land when hauled out with the use of hand-held hoop nets or at sea in tangle nets deployed from boats. After capture, the seals were weighed and sedated with Zoletil (Virbac, Carros, France) at an intramuscular dose rate of 1 mg per 100 kg. Skin samples were collected from the tail using pig-ear notchers and stored at −20°C until analysis. In addition, samples were obtained from harbour seals in France, the Dutch Wadden Sea, and eastern Norway for comparison (Table 1).

TABLE 1 Characteristics of the sampling localities, sizes and dates for the study

Locality	Abbr.	N	Males	Females	Unknown	Sampling Dates
Strangford Lough	SL	17	9	8		2008 & 2010
Islay/Jura	IJ	22	13	8	1	2003
Lismore	LI	19		19		2007
Arisaig	AR	10	5	5		2009
Skye	SK	14	8	6		2004
Outer Hebrides	OH	16	8	8		2006
Pentland Firth	PF	5	4	1		2011
Orkney	OR	44	23	21		2006, 2008 & 2009
Shetland	SH	19	14	5		2010
Moray Firth	MF	34	9	25		2003, 2008 & 2009
Tay and Eden Estuaries	TE	21	10	10	1	2001, 2002, 2003 & 2008
The Wash	WA	20	8	11	1	2003, 2004 & 2005
Blakeney	BL	10		10		2010
Thames	TH	5	5			2006
Chichester Harbour	CH	4	3	1		2009
France	FR	3	2	1		2007
The Netherlands	NE	11	7	3	1	2006, 2008 & 2009
Norway	NO	25			25	
Total		299				

2.2 | DNA extraction and microsatellite genotyping

Genomic DNA was extracted from the skin samples using a salt saturated DNA extraction method (Sunnucks & Hales, 1996). The extracted DNA was quantified in a Nanodrop ND-1000 spectrophotometer and diluted to a working concentration of 10 ng μL^{-1}. The microsatellite loci were divided into four different loci groups and amplified with a Multiplex PCR kit from QIAGEN following the manufacturer's instructions. Briefly, the initial PCR conditions were the same for the four loci groups and consisted of 20 ng of genomic DNA, 5 μL of multiplex mix and 3 μL of primer mix in a 10 μL reaction. The PCR profile was as follows: 95°C for 15 min followed by 30 cycles of 94°C for 30 s, 60°C for 90 s and 71°C for 45 s, with a final extension of 72°C for 2 min. The resulting PCR products were run on a Beckman Coulter capillary electrophoresis instrument and the microsatellite genotypes determined manually using the software GeneMapper (Applied Biosystems, UK). All microsatellite loci were tested in Micro-checker (van Oosterhout, Hutchinson, Wills, & Shipley, 2004) to check for genotyping inconsistencies, large allele dropout, null alleles and stutter bands.

2.3 | Population structure

All analyses were conducted on two datasets; a full dataset with 12 loci, 299 animals and 13% missing data, and a reduced dataset with seven loci, 295 animals, and only 3% missing data. The five loci were excluded from the dataset because they were characterized by high levels of missing data and were flagged by the MICROCHECKER program to have a high probability of stuttering and/or null alleles.

The presence of genetic structure within UK and mainland European harbour seals was assessed by cluster analyses using the program STRUCTURE 2.3.4 (Hubisz, Falush, Stephens, & Pritchard, 2009; Pritchard, Stephens, & Donnelly, 2000). Analyses were performed under the admixture model, using the model of correlated allele frequencies between clusters and locations as priors. For each value of *K* from 1 to 10, five runs were performed, each with 100000 initial steps of burn-in followed by 1 000 000 iterations. To minimize the potential effects of isolation by distance, analyses were also conducted on two geographically defined subsets of the data comprising the northern UK localities and the southern UK and mainland Europe localities. Output data were processed in STRUCTURE HARVESTER (Earl, 2009) and CLUMPP (Jakobsson & Rosenberg, 2007) and graphically displayed using DISTRUCT (Rosenberg, 2004). As inference of the number of clusters *K* can be difficult under scenarios of extensive admixture and isolation by distance (IBD) (Falush, Stephens, & Pritchard, 2003; Pritchard et al., 2000) Evanno's Δ*K* was applied as an additional predictor of *K* (Evanno, Regnaut, & Goudet, 2005).

In addition, in order to estimate the degree of genetic differentiation within and between clusters inferred by STRUCTURE, ARLEQUIN ver. 3.5.1.2 (Excoffier & Lischer, 2010) and FSTAT ver. 2.9.3.2 (Goudet, 1995) were used to obtain pairwise estimates of F_{ST} between sampling localities.

2.4 | Genetic diversity

For each of the clusters inferred by STRUCTURE expected and observed heterozygosity (H_E and H_O) were estimated for each locus using ARLEQUIN ver. 3.5.1.2 (Excoffier & Lischer, 2010) and the allelic richness was calculated with FSTAT ver. 2.9.3.2 (Goudet, 1995), while GENEPOP (Rousset, 2008) was used to test for deviations from Hardy–Weinberg expectations and for linkage disequilibrium. Sequential Bonferroni corrections were applied to assess significance values (Rice, 1989).

Finally, given the recent decline in harbour seal populations in north-eastern UK the Wilcoxon and the sign tests implemented in the program BOTTLENECK v. 1.2 (Piry, Luikart, & Cornuet, 1999) were used to test for recent bottlenecks. Both tests were run under the stepwise mutation model (SMM), and – since microsatellite markers may not be strictly defined by the SMM, but may experience mutational jumps according to the infinite allele mutation model (IAM) – the two-phase mutation model (TPM) was also applied allowing for 95% single-step mutations and 5% multi-step mutations following the recommendations of Piry et al. (1999). Tests were applied separately to samples from Orkney, Shetland, Moray Firth and Tay-Eden Estuaries using both the full and reduced datasets.

3 | RESULTS

3.1 | Population structure

The results from the STRUCTURE analyses were similar for the full and the reduced datasets. They both suggested an initial division into two main groups consisting of localities in northern UK and southern UK–mainland Europe, respectively (Figure 1a), with strong support from both likelihood and Δ*K* values (Supporting Table S1). Within these, the northern cluster was further divided into a north-western cluster consisting of localities from Stangford Lough (SL) in Northern Ireland north to the Outer Hebrides (OH) and further to Pentland Firth (PF), and a north-eastern cluster from Shetland (SH) and Orkney (OR) south to the Tay and Eden estuaries (TE) (Figure 1b,d). The third, south-eastern cluster consisted of southern UK haul-out sites from Chichester harbour (CH) to the Wash (WA), including sites in France (FR) and the Dutch Wadden Sea (NE), whereas the Norwegian (NO) harbour seals appeared to form a separate fourth cluster (Figure 1c).

The four major genetic clusters were characterized by high inter-cluster F_{ST} values (Table 2), but also show indications of further genetic structuring as evident from the pairwise F_{ST} estimates among sampling localities (Supporting Table S2). Overall F_{ST} was 0.097 (95% CI: 0.071–0.127) with a range from 0 to 0.2923 for pairwise comparisons. All pairwise comparisons among sampling localities were significantly different, except for the north-western localities of Islay/Jura, Lismore, Arisaig and Skye (average F_{ST} = 0.0316), as well as localities in south-eastern UK, France and the Dutch Wadden Sea (average F_{ST} = 0.0353), which were characterized by relatively low levels of pairwise genetic differentiation.

3.2 | Genetic diversity

Within the four clusters detected by STRUCTURE, observed heterozygosity (H_O) ranged from 0.448 to 0.508 for the north-eastern UK and Norway, respectively, whereas the average number of alleles ranged

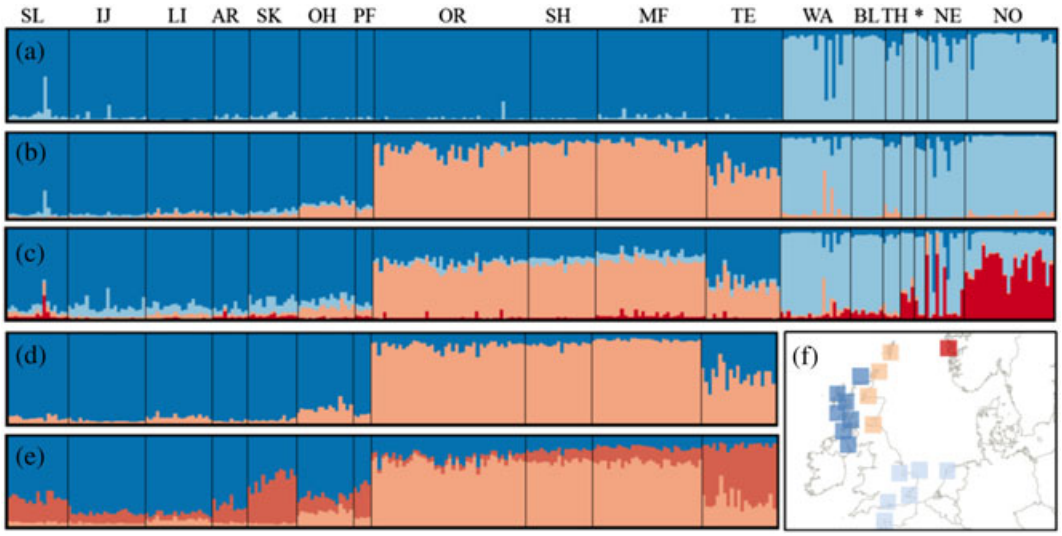

FIGURE 1 Genetic structure of harbour seals in the UK and neighbouring localities on mainland Europe estimated using the reduced dataset (7 loci; 295 animals; 3% missing data) in the program STRUCTURE ver. 2.3.4 (Hubisz et al., 2009; Pritchard et al., 2000). Each vertical bar represents a sampled individual and the colouring its proportion of membership in each of *K* clusters. (a-c) Plots for *K* = 2–4 for all 18 localities showing division between north-western (dark blue) and north-eastern (light red) harbour seal populations in the UK, as well as south-eastern UK, France and the Dutch Wadden Sea (light blue) and Norway (dark red). (d-e) Plots for *K* = 2–3 for the analyses of the northern UK subset. (f) Geographical distribution of the four main genetic clusters. Locality abbreviations are listed in Table 1

TABLE 2 Pairwise F_{ST} comparisons obtained using the distance method based on number of different alleles implemented in ARLEQUIN (above diagonal) and Weir and Cockerham's estimate implemented in GENEPOP (below the diagonal). All F_{ST} comparisons were statistically significant at $P < 0.01$

	North-western UK	North-eastern UK	South-eastern UK	Norway
North-western UK		0.058	0.121	0.178
North-eastern UK	0.044		0.157	0.174
South-eastern UK	0.117	0.160		0.095
Norway	0.155	0.159	0.102	

from 3.5 to 4.9 (Table 3). Several of the microsatellite loci exhibited a significant deficit of heterozygotes within the four clusters, and none of the north-eastern UK localities tested in the BOTTLENECK program carried genetic evidence of recent bottlenecks.

4 | DISCUSSION

4.1 | Genetic clusters

This study presents the first fine-scale analysis of harbour seal population genetic structure and genetic diversity in the United Kingdom and neighbouring localities on the European mainland. In line with the results of Goodman (1998), the analysis of population structure suggested an initial division into two main genetic clusters consisting of localities in the northern UK and the southern UK–mainland Europe (Figure 1a). Within these, however, there was support for additional population structuring, with the northern cluster being divided into a north-western cluster consisting of localities from Strangford Lough in Northern Ireland north to the Outer Hebrides and further to Pentland Firth, and a north-eastern cluster from Shetland and Orkney south to the Tay and Eden estuaries (Figure 1b,d). Similarly, the southern UK–mainland Europe cluster was split into a south-eastern UK cluster consisting of haul-out sites from the Wash to Chichester harbour, including sites in France and the Dutch Wadden Sea, whereas the Norwegian harbour seals appeared to form a separate fourth cluster (Figure 1c). This Norwegian cluster appeared more closely genetically related to harbour seals at localities in south-eastern UK and mainland Europe, than the geographically closer Shetland and Orkney, suggesting limited gene flow across the northern North Sea.

The STRUCTURE analyses gave rise to a few curious observations, with some localities sharing a degree of cluster membership despite being separated by relatively long geographical distances. For example, the Tay and Eden, Strangford Lough, Arisaig, Skye and Pentland Firth localities all share a 'dark orange' component (Figure 1e), and the Outer Hebrides appear to share a 'light orange' component with localities in the north-eastern cluster (Figure 1e). Such observations could result from contemporary movement patterns among geographically distant northern UK harbour seal localities. However, although harbour seals may undertake long distance foraging trips (Tougaard, Teilmann, & Tougaard, 2008), they are typically regarded as relatively philopatric (Dietz et al., 2012; Olsen et al., 2014; Sharples et al., 2012). Thus, it seems more plausible that these observations result from incomplete lineage sorting of ancestral populations, or lack of sufficient resolution in the data.

TABLE 3 Characteristics of the 12 microsatellite loci for each of the four main genetic clusters identified in the analyses

	North-western UK (N = 103)					Northern-eastern UK (N = 118)					South-eastern UK (N = 54)					Norway (N = 25)				
	Na	*Ar*	H_O	H_E	F_{IS}	*P*	*Na*	*Ar*	H_O	H_E	F_{IS}	*P*	*Na*	*Ar*	H_O	H_E	F_{IS}	*P*	*Na*	*Ar*	H_O	H_E	F_{IS}	*P*
OrFCB8*	4	3.8	0.464	0.591	0.216	0.004	4	3.4	0.484	0.592	0.183	0.006	4	3.8	0.460	0.559	0.179	0.110	5	5.0	0.480	0.684	0.303	0.038
Pvc78*	3	2.2	0.379	0.463	0.183	0.098	3	2.4	0.174	0.189	0.082	0.008	4	3.6	0.019	0.198	0.904	0.000	3	3.0	0.040	0.117	0.662	0.020
Lc28*	3	2.9	0.359	0.505	0.290	0.000	3	2.2	0.322	0.337	0.045	0.671	5	4.2	0.096	0.199	0.520	0.000	3	3.0	0.160	0.223	0.286	0.129
Sgpv11*	3	2.2	0.369	0.361	-0.020	1.000	4	3.4	0.314	0.354	0.114	0.262	5	3.9	0.509	0.538	0.053	0.024	3	3.0	0.600	0.541	-0.110	0.512
Hg6.3*	4	3.9	0.624	0.652	0.044	0.416	4	3.6	0.500	0.502	0.004	0.914	6	5.1	0.660	0.656	-0.007	0.022	4	4.0	0.520	0.690	0.250	0.160
Lc26*	4	2.5	0.314	0.469	0.332	0.001	3	3.0	0.509	0.622	0.183	0.028	6	4.4	0.235	0.499	0.531	0.000	3	3.0	0.320	0.422	0.246	0.197
ZcwA12*	5	3.5	0.388	0.387	-0.002	0.017	4	3.2	0.351	0.479	0.268	0.000	4	3.9	0.396	0.592	0.333	0.001	3	3.0	0.480	0.659	0.275	0.145
Lw11	4	2.7	0.143	0.182	0.216	0.064	3	2.3	0.309	0.307	-0.006	1.000	3	2.4	0.057	0.057	-0.007	1.000	3	3.0	0.440	0.451	0.026	0.150
Sgpv10	3	3.0	0.338	0.530	0.365	0.000	3	2.9	0.229	0.324	0.294	0.000	4	3.7	0.175	0.324	0.463	0.000	2	2.0	0.520	0.510	-0.020	1.000
Lw7	5	4.7	0.703	0.725	0.031	0.114	4	3.8	0.545	0.590	0.077	0.002	6	5.8	0.639	0.697	0.084	0.003	6	6.0	0.680	0.787	0.138	0.269
Lw20	5	4.0	0.405	0.374	-0.080	0.185	4	3.2	0.264	0.275	0.040	0.599	4	3.5	0.239	0.289	0.174	0.001						
Hgdii	9	7.9	0.103	0.826	0.877	0.000	11	8.9	0.148	0.804	0.817	0.000	8	8	0.125	0.810	0.849	0.000						
Overall	4.3	3.6	0.382	0.506	0.245		4.1	3.5	0.346	0.448	0.229		4.9	4.4	0.301	0.451	0.337		3.5	3.5	0.424	0.508	0.169	

N = number of individuals; *Na* = number of alleles; *Ar* = allelic richness; H_O = Observed heterozygosity; H_E = Expected heterozygosity; F_{IS} = Inbreeding coefficient within populations; *P* = *P*-value for Hardy–Weinberg tests. The seven loci included in the reduced dataset (7 loci; 295 animals; 3% missing data) are marked with an asterisk, whereas the remaining five loci only were included in the full dataset (12 loci; 299 animals; 13% missing data).

4.2 | Fine-scale population structure

On a finer spatial scale, several of the analyses point to the existence of additional population structuring within each cluster. First, each of the three UK clusters was characterized by high positive F_{IS} values and a significant deficit of heterozygotes, which presumably are due to Wahlund effects. Second, both pairwise estimates of F_{ST} suggested that within the north-western UK cluster, harbour seals in Strangford Lough, the Outer Hebrides and Pentland Firth are different from those at Islay/Jura, Lismore, Arisaig and Skye, among which levels of genetic differentiation were relatively low and statistically insignificant. In the north-eastern UK, pairwise estimates of genetic differentiation were higher and significant among all sampling localities, suggesting limited movements among these. In contrast, localities in the south-eastern UK, France and Dutch Wadden Sea were generally characterized by low levels of genetic differentiation, perhaps reflecting movements between Dutch, French and south-eastern UK haul-out sites.

4.3 | Genetic diversity

Genetic diversity in UK harbour seals was similar or slightly higher than those reported for other European harbour seal populations (Andersen et al., 2011; Olsen et al., 2014), and none of the Orkney, Shetland, Moray Firth and Tay-Eden Estuaries sampling sites tested in BOTTLENECK carried genetic signatures of recent bottlenecks. Genetic and archaeological material suggests that harbour seals colonized northern Europe 10 000 years ago (Goodman, 1998; Härkönen, Harding, Goodman, & Johannesson, 2003; Sommer & Benecke, 2003) and it is likely that associated and subsequent founder effects rather than recent population declines have shaped the main patterns of genetic variation.

4.4 | Implications for management

The Scottish and English harbour seal populations have been divided into 11 management areas based on the distribution of haul-outs and breeding sites, as well as information from tagging data (SCOS, 2014). The results of the genetic analyses reported here lend support to the delineation of these areas, pointing to the existence of three major genetic clusters in the UK, as well as several more fine-scale genetic units (Figure 2). However, at some points, the genetic results contrast with the existing management units. First, the genetic results leave some uncertainty about the current division of the south-western (Islay/Jura) and western Scottish (Lismore, Arisaig and Skye) harbour seal sites into two separate management areas, which, from a genetic point of view, seem to be connected. Second, it seems that the harbour seals in the Pentland Firth, despite being geographically closer to Orkney, with which they currently form a management area, are genetically closer to north-western UK harbour seals, such as those in the Outer Hebrides. This suggests limited spread between Pentland Firth and Orkney and that the management and conservation status of the Pentland Firth harbour seals may have to be reconsidered. Finally, the genetic analysis does not include seals from north-east England, which constitutes a separate management area, leaving this area's status uncertain.

The remaining question is to what extent the genetic results can be used to inform management decisions? Although genetic data are

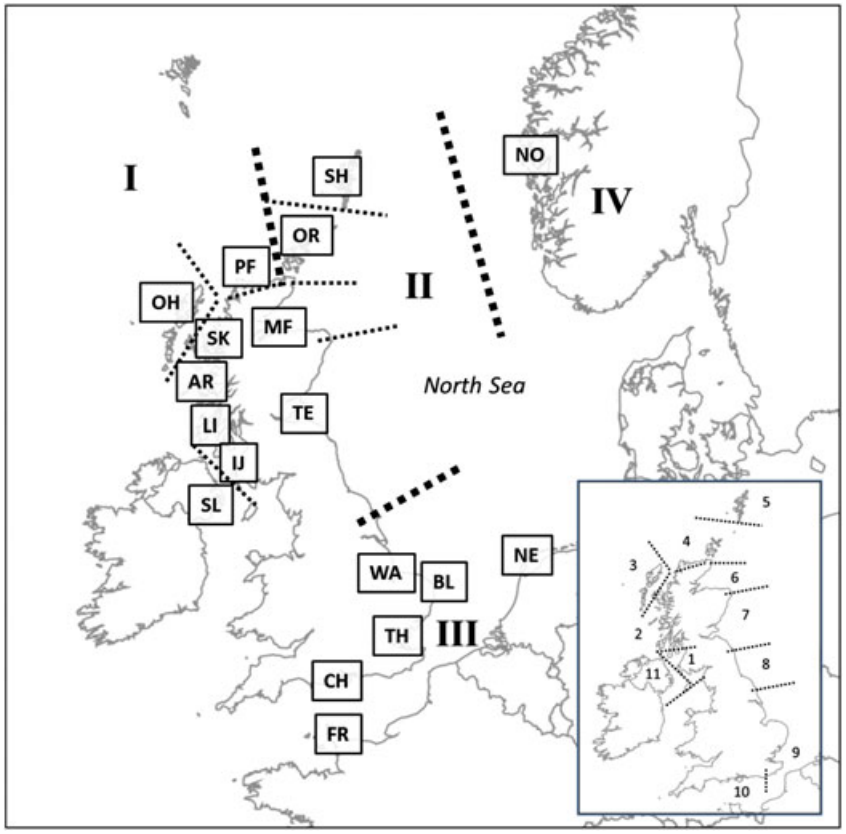

FIGURE 2 Population genetic structuring among harbour seals in the UK and neighbouring localities, showing the major genetic clusters identified in STRUCTURE (thick stippled lines) and minor but statistical significant levels of genetic differentiation estimated by F_{ST} and the exact G-test (thin stippled lines). The major clusters can be interpreted as separate genetic lineages, whereas the finer scale genetic structure is likely due to some degree of demographic and/or ecological separation

often used for the identification of management units, genetic patterns may not reflect the contemporary ecological and demographic patterns typically of interest for management (Lowe & Allendorf, 2010; Palsbøll et al., 2007; Waples & Gaggiotti, 2006). The two genetic datasets used in the present study are characterized by a moderate to relatively high proportion of missing data (12 loci; 299 animals; 13% missing data) or a relatively low number of loci (7 loci, 295 animals, 3% missing data), respectively. Thus the quality and/or power of the genetic analyses may not be adequate for a full understanding of the population structure of UK harbour seals. That said, a recent study on harbour seals in Denmark and Sweden showed a good match between the population structure inferred from genetic (15 microsatellite loci) and ecological (tagging) data, respectively (Olsen *et al*., 2014). It further showed that the inferred genetic populations could be regarded as separate demographic entities and thus serve as management units. Similarly, an overall agreement between the genetic results and the existing management areas for UK harbour seals was observed here. This suggests that an adaptive management approach (Holling, 1978; McLain & Lee, 1996) should be adopted for UK harbour seals, in which the delineation of the current management areas is maintained until further genetic and ecological information on movements and population dynamics has been accumulated.

4.5 | The next steps?

Future studies would certainly benefit from including more genetic data from north-east England and Ireland, as well as further neighbouring sites in Europe, to obtain a more complete understanding of harbour seal genetic structure in the British Isles and how that may connect with the north-eastern European population structure. This could include an integration of microsatellite data from published studies (Andersen et al., 2011; Olsen et al., 2014), and/or the generation of novel genome-wide single nucleotide polymorphism (SNP) data, as has been carried out for other marine mammals (Cammen et al., 2016). The latter approach would not only provide detailed information on harbour seal population structure and movement or migration patterns, but would also facilitate further research, exploring aspects such as local adaptation and pathogen susceptibility. For example, Hammond, Guethlein, Norman, and Parham (2012) found significant regional differences in UK harbour seal MHC class I genes, which are particularly important in regulating the immune response against viral infections. However, a limited number of individuals were included in their study and further work is required to determine how important such differences are at the population level and particularly in predicting their response to viral epidemics, such as phocine distemper. This level of genetic detail would thus allow for the development of bespoke conservation and management strategies, accounting for the specific characteristics of each population or management unit.

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REFERENCES

Andersen, L. W., & Olsen, M. T. (2010). Distribution and population structure of North Atlantic harbour seals (*Phoca vitulina*). *NAMMCO Scientific Publications*, *8*, 15–36.

Andersen, L. W., Lydersen, C., Frie, A. K., Rosing-Asvid, A., Hauksson, E., & Kovacs, K. M. (2011). A population on the edge: Genetic diversity and population structure of the world's northernmost harbour seals (*Phoca vitulina*). *Biological Journal of the Linnean Society*, *102*, 420–439.

Cammen, K. M., Andrews, K. R., Carroll, E. L., Foote, A. D., Humble, E., Khudyakov, J. I., … VanCise, A. M. (2016). Genomic methods take the plunge: Recent advances in high-throughput sequencing of marine mammals. *Journal of Heredity*, *107*, 481–495.

Dietz, R., Teilmann, J., Andersen, S. M., Rigét, F., & Olsen, M. T. (2012). Movements and site fidelity of harbour seals (*Phoca vitulina*) in Kattegat, Denmark, with implications for the epidemiology of the phocine distemper virus. *ICES Journal of Marine Science*, *69*, 1–10.

Earl, D. A. (2009) STRUCTURE HARVESTER version 0.3. Available online at http://users.soe.ucsc.edu/~dearl/software/struct_harvest/.

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, *14*, 2611–2620.

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, *10*, 564–567.

Falush, D., Stephens, M., & Pritchard, J. (2003). Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, *164*, 1567–1587.

Goodman, S. J. (1998). Patterns of extensive genetic differentiation and variation among European harbor seals (*Phoca vitulina vitulina*) revealed using microsatellite DNA polymorphisms. *Molecular Biology and Evolution*, *15*, 104–118.

Goudet, J. (1995). FSTAT (Version 1.2): A computer program to calculate F-statistics. *Journal of Heredity*, *86*, 485–486.

Hammond, J. A., Guethlein, L. A., Norman, P. J., & Parham, P. (2012). Natural selection on marine carnivores elaborated a diverse family of classical MHC class I genes exhibiting haplotypic gene content variation and allelic polymorphism. *Immunogenetics*, *64*, 915–933.

Härkönen, T., Harding, K. C., Goodman, S. J., & Johannesson, K. (2005). Colonization history of the Baltic harbour seals: Integrating archaeological, behavioral, and genetic data. *Marine Mammal Science*, *21*, 695–716.

Holling, C. S. (1978). *Adaptive environmental assessment and management*. New York: John Wiley & Sons.

Hubisz, M. J., Falush, D., Stephens, M., & Pritchard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, *9*, 1322–1332.

Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23*, 1801–1806.

Lowe, W. H., & Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology*, *19*, 3038–3051.

McLain, R., & Lee, R. (1996). Adaptive management: Promises and pitfalls. *Environmental Management*, *20*, 437–448.

Moritz, C. (1994). Defining evolutionary significant units for conservation. *Trends in Ecology & Evolution*, *9*, 373–375.

Olsen, M. T., Andersen, L. W., Dietz, R., Teilmann, J., Härkönen, J., & Siegismund, H. R. (2014). Integrating genetic data and population viability analyses for the identification of harbour seal (*Phoca vitulina*) populations and management units. *Molecular Ecology*, *23*, 815–831.

Palsbøll, P. J., Bérubé, M., & Allendorf, F. W. (2007). Identification of management units using population genetic data. *Trends in Ecology & Evolution*, *22*, 11–16.

Piry, S., Luikart, G., & Cornuet, J.-M. (1999). Computer note. BOTTLENECK: A computer program for detecting recent reductions in the effective size using allele frequency data. *Journal of Heredity*, *90*, 502–503.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*, 945–959.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution*, *43*, 223–225.

Rosenberg, N. A. (2004). DISTRUCT: A program for the graphical display of population structure. *Molecular Ecology Notes*, *4*, 137–138.

Rousset, F. (2008). genepop'007: A complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources*, *8*, 103–106.

SCOS (Special Committee on Seals). (2014). Scientific Advice on Matters Related to the Management of Seal Populations 2014. http://www.smru.st-and.ac.uk/documents/2259.pdf, p. 161.

Sharples, R. J., Moss, S. E., Patterson, T. A., & Hammond, P. S. (2012). Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. *PLoS ONE*, *7*, e37216.

Sommer, R., & Benecke, N. (2003). Post-glacial history of the European seal fauna on the basis of sub-fossil records. *Beitraege zur Archaeozoologie und Praehistorischen Anthropologie*, *4*, 16–28.

Stanley, H. F., Casey, S., Carnahan, J. M., Goodman, S., Harwood, J., & Wayne, R. K. (1996). Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*). *Molecular Biology and Evolution*, *13*, 368–382.

Sunnucks, P., & Hales, D. F. (1996). Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus *Sitobion* (Hemiptera: Aphididae). *Molecular Biology and Evolution*, *13*, 510–524.

Tougaard, J., Teilmann, J., & Tougaard, S. (2008). Harbour seal spatial distribution estimated from Argos satellite telemetry: Overcoming positioning errors. *Endangered Species Research*, *4*, 113–122.

van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., & Shipley, P. (2004). Micro-Checker: Software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, *4*, 535–538.

Waples, R. S. (1998). Evolutionarily significant units, distinct population segments, and the endangered species act: Reply to Pennock and Dimmick. *Conservation Biology*, *12*, 718–721.

Waples, R. S., & Gaggiotti, O. (2006). What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, *15*, 1419–1439.

Westlake, R. L., & O'Corry-Crowe, G. M. (2002). Macrogeographic structure and patterns of genetic diversity in harbour seals (*Phoca vitulina*) from Alaska to Japan. *Journal of Mammalogy*, *83*, 1111–1126.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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